

## Seasonal variations of Collembola (Hexapoda) assemblages in damp riparian habitats

Sithan Lek-Ang\* and Louis Deharveng<sup>1</sup>

With 8 figures, 3 tables and 1 appendix

**Abstract:** The changes in species richness and abundance of Collembola in two Pyrenean springs (Ruau and La Maure) were evaluated bimonthly on an annual cycle, comparing the hydrophilous and non-hydrophilous population components. Low species richness and high abundance of the hydrophilous component was a constant feature of the studied assemblages. The non-hydrophilous component (forest and meadow litter species) exhibited much higher richness and lower abundance. Seasonal fluctuations in species richness were moderate and highly correlated between the two springs for the non-hydrophilous component (discarding the aberrant April data of Ruau), but not for the hydrophilous component. A high proportion of juveniles was encountered throughout the year. Abundance peaked in June, in association with an increase in juvenile recruitment, and was minimum in August (Ruau) or December (La Maure). The observed biodiversity patterns may result from a combined effect of evolutionary and habitat-dependent factors according to the following hypotheses: (i) hydrophilous Collembola always have a lower diversity than mesophilous ones, which presumably implies that the group tends to speciate less in damp habitats, i.e. at the limit of its ecological range; (ii) the spatial configuration of the damp habitats studied (small patches around springs and narrow strips along streams), as well as the non-saturation of communities due to frequent ecological resets after flooding, determine a high permeability to outside colonizers; (iii) high fertility, in the absence of individual adaptation, acts as a population-level response to constraints imposed by periodical flooding; (iv) water acts as a thermal and humidity buffer making hydrophilous species assemblages less dependent on climatic fluctuations; (v) for the same reason, damp habitats constitute refugia for invertebrates when surrounding environments are affected by drought, warmth or cold. This last feature might give damp habitats a central function in the dynamics of the larger terrestrial ecosystems in which they are nested.

<sup>1</sup> **Authors' addresses:** UMR 5552 du CNRS-Laboratoire d'Ecologie Terrestre, Université Paul Sabatier, 118 route de Narbonne, 31062 Toulouse cedex 4 (France). E-mail: ang@cict.fr

\* Corresponding author.

**Key words:** Collembola, Pyrenees, riparian habitats, habitat permeability, seasonal dynamics.

## Introduction

Whereas the aquatic/terrestrial ecotone has often been analysed regarding its geomorphology, physico-chemical properties and vegetation, little has been published about the invertebrate assemblages of the terrestrial side of the ecotone. In the overview of GREGORY et al. (1992), the role of terrestrial animal populations as bioturbators or food resources for aquatic biota is not even mentioned, though field observations and the limited relevant literature unambiguously points to its functional importance (GIBERT 1986, WARD et al. 1998). Damp riparian habitats are inhabited by many arthropod lineages, most of terrestrial origin, including Trichoniscidae, a large family of Oniscidea isopods (VANDEL 1960); several Caraboidea beetles (FRÄMBS 1994); and larval stages of Diptera (THOMAS 1969). This last group usually dominates the specialised fauna of damp habitats in biomass, while springtails (Collembola) are frequently the most abundant arthropods. A number of springtail species are strictly associated with permanent water-saturated substratum, particularly among the genera *Isotomurus* and *Sminthurides*. *Podura aquatica* LINNÉ, typically lives on the surface of ponds. Species of these hydrophilous taxa tend to live in dense populations on the water/terrestrial ecotone. The subsurface sediments, closer to the water-table, host other, poorly known species (CHRISTIAN 1986, BRETSCHKO & CHRISTIAN 1989, WARD et al. 1998 and personal observations along the River Rhône). The hydrophobic properties of Collembolan cuticles (NOBLE-NESBITT 1963, HOPKIN 1997) probably give them a decisive advantage to cope with life in wet habitats compared to many other terrestrial invertebrates. Because of this feature, they can tolerate flooding and easily disperse along streams on the water surface, where they may constitute an important component of drift organisms (GIBERT 1986), usually overlooked in the literature (MASON & MACDONALD 1982).

The diversity of hydrophilous Collembola has been considered moderate for a long time. For instance, about 12 species may be categorised as hydrophilous out of a total of 206 recorded by CASSAGNAU (1961) in the Central Pyrenees, one of the best studied areas in Europe. This low diversity is challenged however by recent taxonomic studies. In particular, the most widespread hydrophilous taxon of temperate climates, *Isotomurus palustris* MÜLLER, long considered as a single polychromatic species, has been recently shown to represent a cluster of species (CASSAGNAU 1987, DEHARVENG & LEK 1993, CARAPPELLI et al. 1995 a). As many as 6 species of this genus may even co-occur at the same site (CARAPPELLI et al. 1995 b). Taxonomic reappraisal of

other collembolan genera rich in hydrophilous species, such as *Pseudisotoma* in the Pyrenees, is currently leading to a marked increase in the number of collembolan species linked to damp habitats. In spite of their numerical importance, and now of their diversity, collembolan assemblages of damp habitats have been the subject of few studies (CASSAGNAU & ROUQUET 1962, HALE 1966, PEDIGO 1970, PRAT & MASSOUD 1981, PICHARD et al. 1989, DEHARVENG & LEK 1995). Furthermore, none of these works concern seasonal variations in their diversity.

This study attempts to explore this issue, i.e., temporal changes in community composition and structure throughout the year. Given the many special features of damp habitats, i.e., permanent saturation of the substratum, filling of deep interstitial crevices by water and buffered thermal variations, it can be assumed that dynamics of their collembolan assemblages should depart from those of soil habitats. In this context, we examined: (i) the main features of collembolan assemblages in these damp riparian habitats; (ii) how abundance and biodiversity of springtails fluctuate during an annual cycle; (iii) the differential responses of the hydrophilous versus non-hydrophilous components to these changes; (iv) how habitat versus climatic variables control collembolan biodiversity fluctuations; and (v) how the peculiarities of the studied damp riparian habitat assemblages may be explained in a broader ecological context.

## Materials and methods

### Study sites

The two springs selected for the study are 1.5 km apart in the Ariège Pyrenees (France). They have different vegetation environments, but are in the same local microclimate and altitudinal range. Both are on calcareous substratum, but only at La Maure are the sampling points directly in contact with limestone rock.

The La Maure spring (0° 44' 13" E, 43° 0' 19" N) arises at 436 m altitude at the edge of a mixed oak forest. Emerging water, which is partially collected in a basin, forms La Maure stream, a small tributary of River Le Job. Flow is perennial, several tens of litres per second most of the year except in summer. During the study period, flow rate was very low in August, with water flowing only low down between the calcareous stones which cover the spring area.

The Ruau spring (0° 44' 13" E, 43° 0' 58" N) is located at 784 m altitude under a line of trees bordering a meadow, on a steep slope. Waters are collected in a small open basin for cattle consumption. Water flow, a few litres/second, is permanent.

### Sampling and species identification

Samples were collected every two months from December 1993 to December 1994. Eighty four substratum cores were taken from each spring. The samples were collected

along four transect lines at each site, and at three distances from open water (in contact with, at  $20 \pm 5$  cm and at  $40 \pm 10$  cm from the water). Each sample contained  $125 \text{ cm}^3$  of damp mosses and superficial soil, sometimes damp moss alone on rocks at La Maure.

The fauna was extracted in the laboratory using Berlese-Tullgren funnels for two weeks, until substratum samples were completely dry. Animals were collected and stored in 90% ethanol. Collembola were sorted and counted under a stereomicroscope. When necessary for identification, individuals were cleared in acetic acid for a few minutes, depending on species pigmentation, and mounted in arabic gum. Morphological observation at high magnification (up to  $\times 1000$ ) was made with a Nomarski contrast Nachet microscope.

Temperature was measured in the field at each sample point, 1 to 2 cm within the substratum. Water content of the substratum was calculated using the difference between fresh and dry weights of sample cores, after drying to constant weight at room temperature (c.  $20^\circ\text{C}$ ) for 15 to 20 days.

### Data analysis

Number of species (species richness) and number of individuals (abundance) per species were evaluated for each sample and calculated for each site and sampling period. In order to evaluate sampling exhaustivity, and in complement to species accumulation curves (*sensu* COLWELL & CODDINGTON 1994), we used the first order jackknife estimate of total species richness:  $S = S_{\text{obs}} + L((n-1)/n)$ , where  $S_{\text{obs}}$  is the number of observed species in the set of samples,  $L$  the number of species which occurred in only one sample, and  $n$  the number of samples (COLWELL & CODDINGTON 1994).

The relative variability of abundance and species richness was measured by the coefficient of variation (Standard deviation / mean).

The similarity of sample assemblages was measured by three indices (MAGURRAN 1988):

Jaccard's coefficient:  $j/(a+b-j)$ ,

Sorensen's coefficient:  $2j/(a+b)$ ,

Morisita's index:  $2 \cdot \Sigma(a_{ni} \cdot b_{ni}) / [(d_a + d_b) \cdot a_N \cdot b_N]$  with  $d_a = \Sigma a_{ni}^2 / a_N^2$  and  $d_b = \Sigma b_{ni}^2 / b_N^2$

where  $j$  = number of species present in both samples A and B;  $a$  = number of species in sample A;  $b$  = number of species in sample B;  $a_{ni}$ ,  $b_{ni}$  = number of individuals of species  $i$  in sample A and sample B;  $a_N$  = total number of individuals in sample A;  $b_N$  = total number of individuals in sample B.

Compared to Jaccard's, Sorensen's coefficient gives more weight to matches than to mismatches in species composition between two samples (KREBS 1989). Morisita index takes into account species abundance, not just presence/absence, and better reflects ecological similarity of the compared samples, giving lower weight to rare species. Linear associations between variables were explored by the Pearson product-moment correlation (VELLEMAN 1997). Datadesk (VELLEMAN 1997) was used for statistical tests.

Analyses were conducted at two scales. Point abundance and point species richness (alpha diversity, MAGURRAN 1988) are the number of individuals and the number of species found in one sample core. Site abundance and site species richness are the abundance and the species richness measured in all samples of a site pooled together.

The assemblages of Collembola were considered both in their totality, and by contrasting their hydrophilous component (species dependent on open water) and their non-hydrophilous component (species independent of open water, mostly mesophilous species from litter and soil). Hydrophilous status was evaluated after the literature (DEHARVENG & LEK 1995).

We also evaluated at sight the proportion of first and second instars versus other juveniles and versus adult and subadult specimens using body size, head / body length ratio, pigmentation intensity when applicable (GREGOIRE-WIBO 1974, THIBAUD 1970) in order to get an idea of the population structure, as juveniles occurred in very large numbers in some samples.

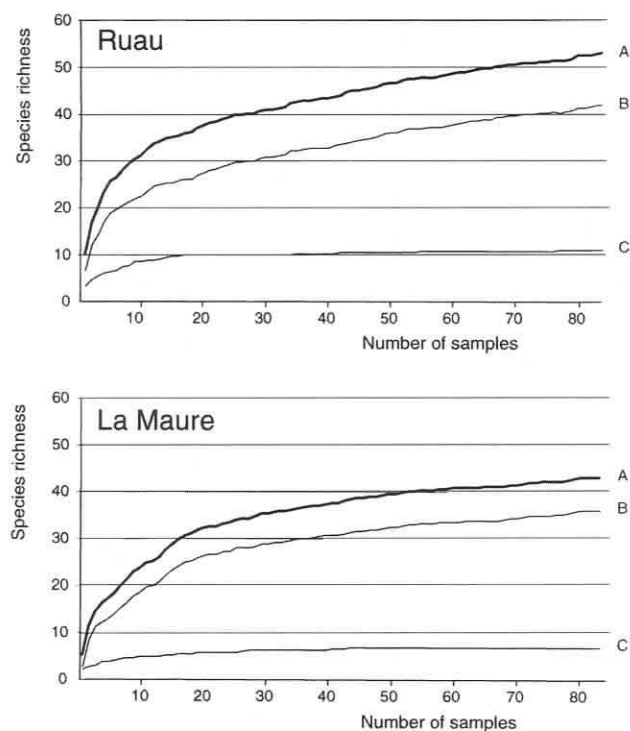
Biological material is stored in the first author's collection. Dataset is available on request from the authors and summarized in the Appendix.

## Results

### General features of Collembola diversity in the study sites

Altogether 59 species of Collembola were collected, of which 53 were present at Ruau and 43 at La Maure (see Appendix). The 11 strictly hydrophilous species of this fauna were all present at Ruau, whereas only 7 were found at La Maure. The remaining 48 non-hydrophilous species were mostly litter or moss inhabitants. Among them, several appear tolerant to water saturation of the substratum: *Folsomia manolachei*, *Isotomiella minor*, *Onychiurus pseudogranulosus* and *Pseudisotoma* sp. 1 at Ruau; *Folsomia manolachei*, *Isotomiella minor*, *Onychiurus pseudogranulosus* and *Protaphorura armata* at La Maure. Fig. 1 illustrates this high permeability of damp riparian habitats to mesophilous species in terms of species diversity, and how little it affects the numerical dominance of hydrophilous taxa.

Similarity between the assemblages of the two springs was rather high (37 species in common, Jaccard similarity index 0.62, Sorensen similarity index 0.77, Morisita similarity index 0.76). A salient feature is the nearly identical overall abundance when pooled over seasons: 10,995 specimens in total at La Maure, 10,076 at Ruau. Point species richness ranged from 1 to 16 species ( $8.3 \pm 4.4$ ) at La Maure, and 1 to 21 species ( $10.6 \pm 3.8$ ) at Ruau. Hydrophilous Collembola reached 57.4 % of the total abundance at Ruau and 56.9 % at La Maure, compared with 20.8 and 16.3, respectively, for species richness (Fig. 1). Thus, Collembolan assemblages seem very similar in their general structure at both springs.



**Fig. 2.** Species accumulation curves, smoothed at 20 iterations, for the total fauna (A), the non-hydrophilous (B), and the hydrophilous (C) components of the two studied assemblages.

**Table 1.** Variability of abundance (number of individuals) and species richness per sampling period of the hydrophilous and non-hydrophilous species sets.

Abundance	Hydrophilous		Non-hydrophilous		Total	
	La Maure	Ruau	La Maure	Ruau	La Maure	Ruau
Mean (M)	898.14	961.28	672.57	471.28	1570.71	1432.57
SD/M	0.78	0.48	0.32	0.43	0.55	0.44
Species richness	Hydrophilous		Non-hydrophilous		Total	
	La Maure	Ruau	La Maure	Ruau	La Maure	Ruau
Mean (M)	4.57	8.14	20.71	22	25.28	30.14
SD/M	0.28	0.11	0.13	0.19	0.14	0.16

comparisons being 6. Fluctuations appear high at Ruau and weak at La Maure (Table 2).

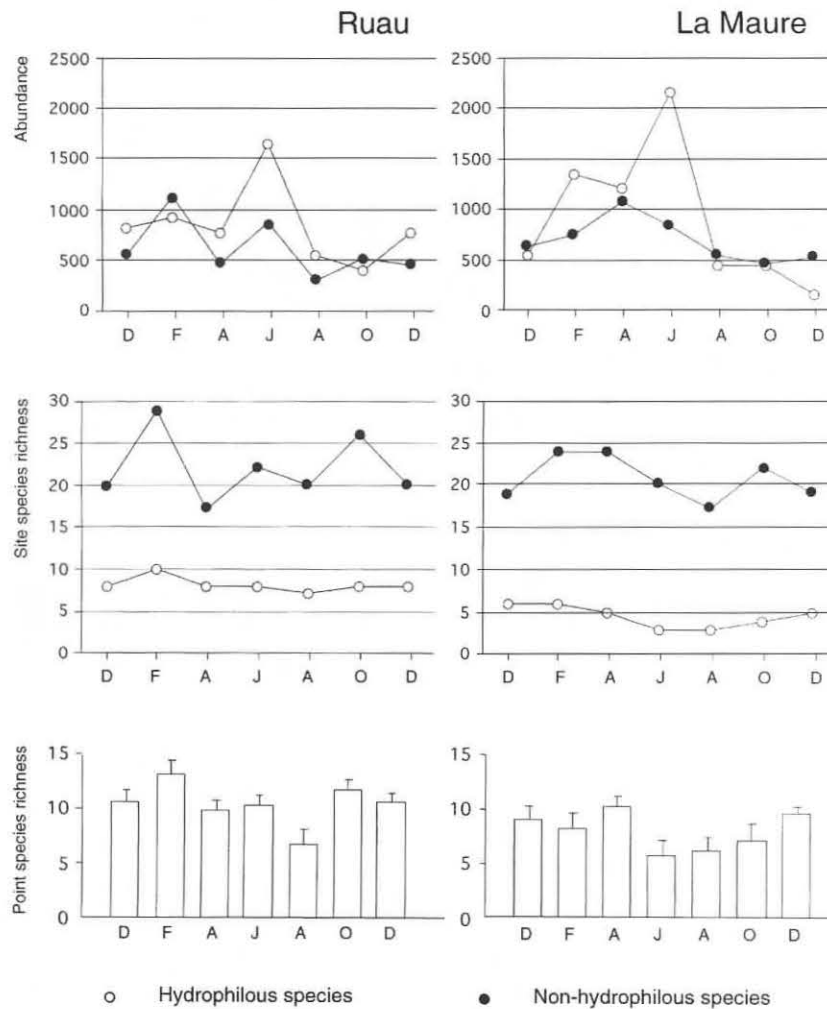
Seasonal transitions in Collembolan assemblages demonstrated marked differences between hydrophilous and non-hydrophilous species (Fig. 3). Hy-

**Table 2.** Differences in mean abundance (number of individuals per sample) and mean species richness (number of species per sample) among sampling periods. Pooled t-test of  $\mu_1 - \mu_2$ ;  $p \leq 0.05$  (\*) and  $p \leq 0.01$  (\*\*)

<b>Abundance</b>							
Ruau	Fe94	Ap94	Ju94	Au94	Oc94	Dec94	
De93	0.1501	0.6993	0.1037	0.1914	0.2244	0.6495	
Fe94		0.0403*	0.5038	0.0052**	0.0053**	0.0247*	
Ap94			0.0496*	0.2314	0.2756	0.9609	
Ju94				0.0138*	0.0154*	0.0415*	
Au94					0.8406	0.1883	
Oc94						0.2216	
La Maure	Fe94	Ap94	Ju94	Au94	Oc94	Dec94	
De93	0.1527	0.0592	0.094	0.702	0.5068	0.2157	
Fe94		0.7484	0.4126	0.0657	0.0315*	0.0091**	
Ap94			0.5153	0.0176*	0.0056**	0.0010**	
Ju94				0.0598	0.0439*	0.0259*	
Au94					0.776	0.3248	
Oc94						0.3478	
<b>Species richness</b>							
Ruau	Fe94	Ap94	Ju94	Au94	Oc94	Dec94	
De93	0.1403	0.6106	0.8214	0.0327*	0.4227	1.0000	
Fe94		0.0344*	0.0634	0.0011**	0.3571	0.0706	
Ap94			0.7400	0.0513	0.1253	0.4951	
Ju94				0.0299*	0.2288	0.7629	
Au94					0.0028**	0.0114*	
Oc94						0.2779	
La Maure	Fe94	Ap94	Ju94	Au94	Oc94	Dec94	
De93	0.6841	0.4401	0.1152	0.1301	0.3503	0.6440	
Fe94		0.2718	0.2765	0.3451	0.6449	0.3890	
Ap94			0.0221*	0.0168*	0.0900	0.6213	
Ju94				0.7730	0.4928	0.0297*	
Au94					0.6315	0.0209*	
Oc94						0.1295	

drophilous Collembola were most abundant in June, the minimum values being from August to December, with a very similar fluctuation pattern at both sites (Pearson 0.847). Conversely, the changes for the non-hydrophilous component of the fauna were unrelated between the two springs (Pearson 0.288), with maxima in February at Ruau and in April at La Maure.

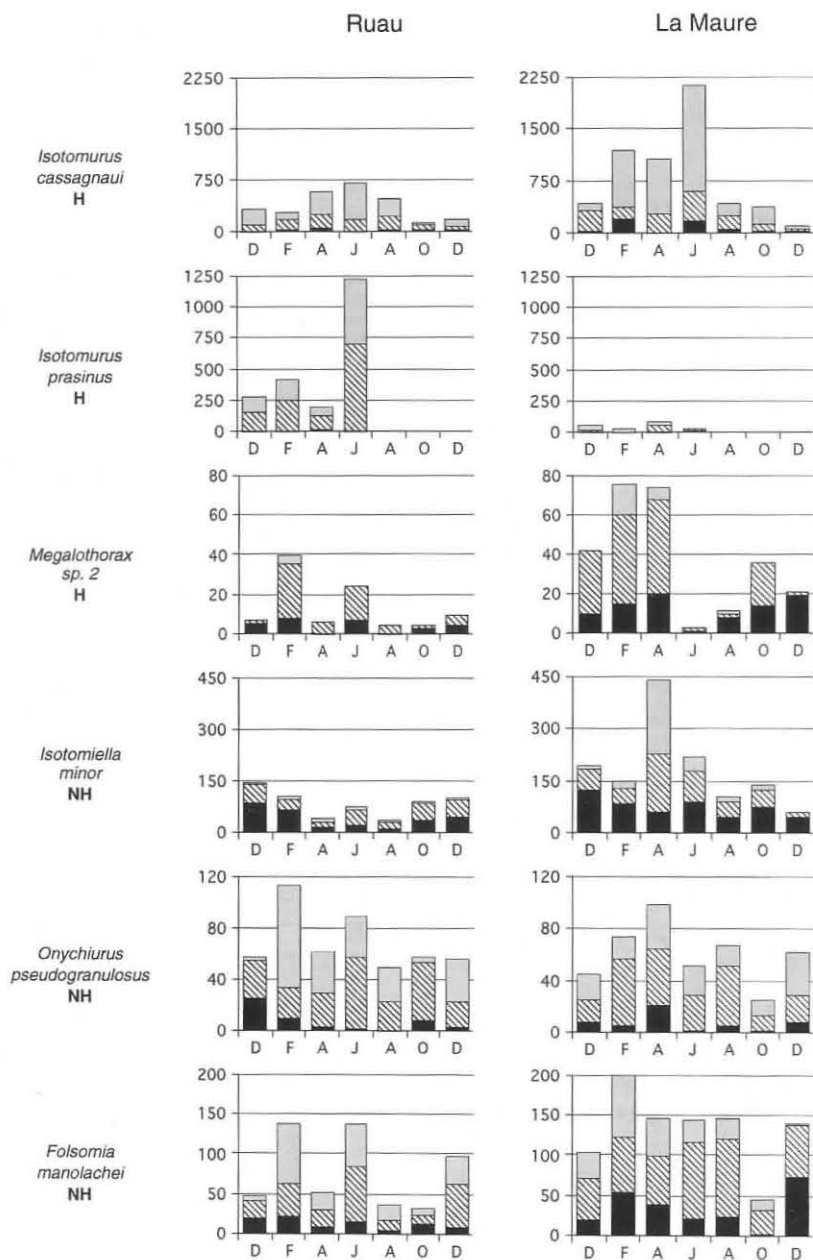
This seasonal pattern is in fact strongly influenced by the disproportionate abundance of a very few species, and by the seasonal pattern of juvenile recruitment. The most abundant species (*Isotomurus cassagnai*) constituted 26.36 % of the total abundance at Ruau, and 51.65 % at La Maure. This hydrophilous species alone is responsible for the high peak of June at La Maure,



**Fig. 3.** Fluctuation in abundance (number of individuals per sampling period) and species richness of hydrophilous versus non-hydrophilous Collembola at Ruau and La Maure. Point (core) species richness: means + SE.

while *Isotomurus prasinus* alone, another hydrophilous species, explains the peak of the same period at Ruau (Figs. 3 and 4). Discarding juvenile specimens from the analysis would further smooth the pattern, since first + second instars largely contributed to seasonal variations at both springs, especially at the highest abundance periods (from 57 to 95 % of the total Collembola abundance, Fig. 5).





**Fig. 4.** Fluctuations of abundance (number of individuals per sampling period) of 6 common species of Collembola in the two springs from December 1993 to December 1994. Grey: first and second instars; hatching: other juveniles; black: adults and sub-adults; H: hydrophilous species; NH: non-hydrophilous species.

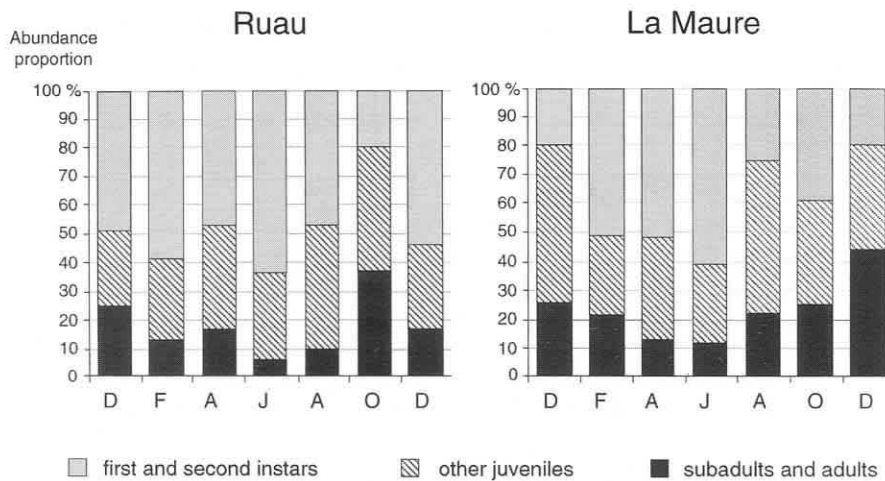


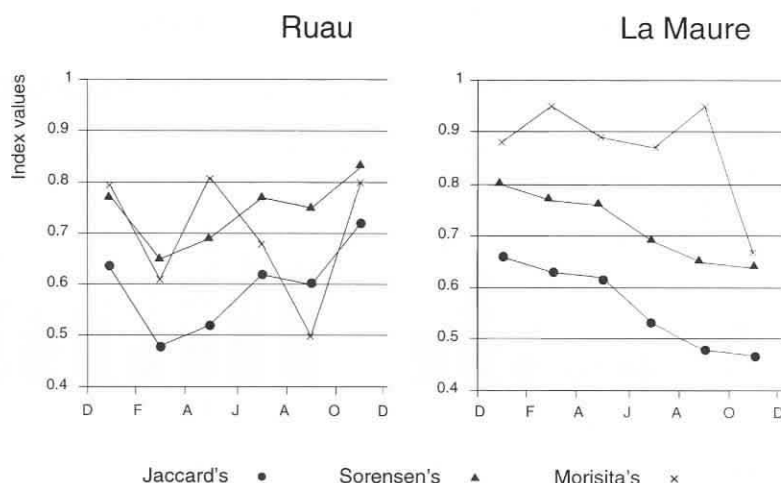
Fig. 5. Relative abundance of life stages of Collembola in the two springs from December 1993 to December 1994.

### Biodiversity fluctuations in the annual cycle

Moderate variations in site species richness during the annual cycle were observed at both sites: 25 to 39 species per sampling period at Ruau, 20 to 30 at La Maure. Ruau and La Maure diversities varied in parallel, with site diversity higher in Ruau except for April. Considered separately, however, the hydrophilous component exhibits a different pattern, and this pattern is not parallel between the two springs (Fig. 3). This is reflected in Pearson correlation coefficients between site species richnesses: they are higher for hydrophilous than for non-hydrophilous species (Pearson: 0.645 against 0.391) when all periods are considered, but the reverse is true with a very high correlation between non-hydrophilous site species richness when the month of April is discarded from the analysis (0.664 against 0.953).

Overall variability of site species richness across the studied period was low at both sites, with a coefficient of variation (SD/M) never reaching 0.30 (Table 1). Its highest value, 0.28, measured at La Maure for the hydrophilous species set, is likely to be related to partial drying up of this spring in summer. Abundances similarly exhibited their highest variation (0.78) at La Maure for the hydrophilous species set.

We measured seasonal changes in point species richness by comparing the means of point species richness among sampling periods (Table 2). Significant differences were found at La Maure between four of the 21 month-to-month cases. Only one of these cases concerns successive periods. Like abundances (see above), species richness can be considered stable throughout the year at this site. At Ruau, differences in species richness are significant or highly sig-



**Fig. 6.** Similarity index values for the collembolan fauna between successive sampling periods, measured by three different indices (Jaccard's, Sorensen's, Morisita's).

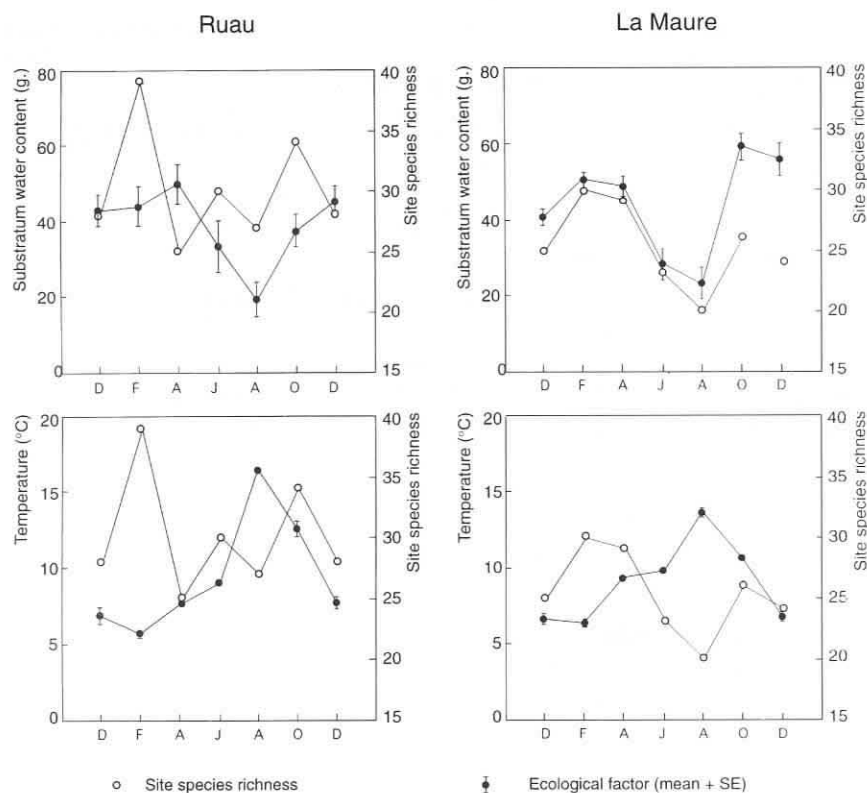
nificant in 6 cases of which 3 concerned successive periods. In spite of a more regular water supply at the Ruau spring, species richness, like abundance, fluctuated more than at La Maure.

### Species turn-over

The complexity of the pattern of biodiversity fluctuations is further illustrated by plotting the successive between-period similarity indices, which reflects the importance of species turn-over (Fig. 6). Jaccard and Sorensen indices which are based on presence/absence of species, vary in parallel at each site, but their pattern at Ruau (decreasing, then roughly increasing similarity over time) strongly differs from that at La Maure (decreasing similarity over time). The Morisita index, which takes in consideration species abundances and better reflects similarity in community structure, has a profile strongly different from both Jaccard's and Sorensen's on one hand. On the other hand, it indicates much higher between-period similarities at La Maure than at Ruau, in agreement with the correlations calculated between successive periods for the mean point species richness analysed above.

### Possible climatic correlations

In spite of some contrasts in the results exposed above, biodiversity roughly fluctuated in parallel at the two sites if we discard the April sampling period (Fig. 7), suggesting a possible common underlying control by regional climatic factors. We tried to explore in more detail how temperature and water



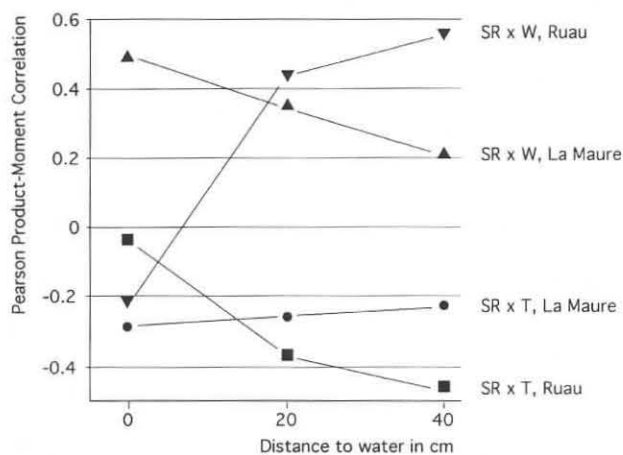
**Fig. 7.** Bimonthly fluctuations of site species richness, water content and temperature of the substratum at the two study sites.

content of the substratum, both highly dependent on climate and strongly influencing collembolan assemblage dynamics (review in HOPKIN 1997), were related to species richness. Pearson product moment correlations were calculated on the 84 samples of each site between abiotic factors, abundances and point species richness (Table 3). In relation to the site configuration, the correlation between water content of the substratum and distance to open water was high at Ruau (where substratum was mainly moss and soil) and low at La Maure (where substratum was mainly moss on rocks) (Table 3). Temperatures were significantly and negatively correlated with water content at both sites (also visible in Fig. 7). Abundances were strongly related to distance to water, negatively at Ruau but positively at La Maure. Correlation of abundance with water content was highly significant at Ruau, but not at La Maure, and correlation with temperature was not significant at both sites.

Correlations of water content with point species richness were non significant at Ruau, weakly significant at La Maure (at  $\alpha = 0.10$ ) in spite of the

**Table 3.** Pearson product moment correlations between distance to water, water content of the substratum, temperature, abundance and point species richness, calculated from 84 samples at each site. \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$

La Maure, N=84	Distance	Water content	Temperature	Abundance
Water content	-0.153			
Temperature	-0.099	-0.340**		
Abundance	0.379***	0.066	-0.046	
Species richness	0.564***	0.200	-0.271*	0.336**
Ruau, N=84	Distance	Water content	Temperature	Abundance
Water content	-0.609***			
Temperature	-0.109	-0.358***		
Abundance	-0.390***	0.365***	-0.184	
Species richness	0.151	0.038	-0.338**	0.133



**Fig. 8.** Correlations between species richness (SR) and substratum temperature (T) or water content (W) at the two study sites, measured at three distances to water.

strikingly parallel fluctuations of site species richness with water content of the substratum at this site (Fig. 7).

Because species richness was more dependent on distance to water than on water content at both sites, and because correlation between distance to water and species richness was highly significant at La Maure (Table 3), we carried out correlation analyses on subsets of samples corresponding to three classes of distance to water (Fig. 8). At both sites, the influence of temperature and water-content on biodiversity changed with distance to water. But, while the correlation between temperature and species richness slightly increased at La Maure with increasing distance to water, it decreased at Ruau; similarly, the

correlation between water content and species richness decreased at La Maure, while it increased at Ruau.

## Discussion

Obtaining a good estimate of species richness required a much higher number of samples for non-hydrophilous than for hydrophilous species in our study. Implication of this simple result for sampling standardization and ecological meaningfulness is important: it means that a same sampling effort in a same habitat may reflect adequately the biodiversity of some organisms but inadequately the biodiversity of others, according to their respective ecological category. Many biodiversity datasets from the literature would deserve to be re-examined from this point of view.

In the present study, collembolan assemblages were structured in a very characteristic way: they exhibited a strong numerical dominance of a few hydrophilous species with high fecundity, associated to a high diversity of non-hydrophilous species that also occurred in surrounding habitats. The former feature accounted for much of the observed abundance fluctuations, while the latter explained much of the biodiversity dynamics.

The low diversity/high abundance of hydrophilous species observed here confirms previous observations in the Pyrenees by DEHARVENG & LEK (1993). Such a pattern is known to characterise extreme habitats (see CASSAGNAU 1961 for Collembola), where a limiting resource constrains assemblage structure. Here, rather than a limiting resource (there is usually plenty of potential food in the epigeous damp habitats), it is the limited access to available resources imposed by water saturation of the substratum which is likely to have generated the observed pattern. Low biological richness is not only a local environment-dependent feature of hydrophilous collembolan assemblages; it also has historical causes. Hydrophilous Collembola belong in fact to a few genera, of which *Sminthurides* and above all *Isotomurus* (CARAPELLI et al. 1995 b) are the most speciose and abundant in temperate damp habitats. This low generic richness characterises all temperate regions examined so far (WEINER 1981, JORDANA et al. 1990, PONGE 1993, SKIDMORE 1995, CHRISTIANSEN & BELLINGER 1998). It can be postulated that the evolutionary shift towards life in permanently humid or saturated habitats has been rare and perhaps a dead-end for Collembola, none of which is adapted to aquatic life.

A high proportion of juveniles was observed throughout the year, which may be a consequence of overlapping life cycles of different species, or of non-seasonal recruitment. In fact, both cases seemed to exist in the studied assemblages. Some species had summer or winter minima, while others maintained active populations throughout the year. This mixed pattern is a general

trend among soil Collembola (HALE 1966, PEDIGO 1970) in contrast to pterygotan Insecta, which are much more season-dependent. The overall collembolan abundance peaked in June and was low from August to December, largely in relation with juvenile recruitment (Figs. 4 and 5). Living in a narrow strip along running water, the populations are affected by frequent floods which are likely to wash away most of the animals. In the absence of mechanical adaptation to this constraint at the individual level, high production of juveniles may constitute an efficient response at the population level for species survival and dispersion.

The seasonal fluctuations recorded here are definitely not congruent with published data on the dynamics of collembolan populations in other natural habitats (HIJII 1987, POZO et al. 1986, HALE 1966, PEDIGO 1970). However, most of these literature datasets are mutually incongruent as well. The fact that authors usually did not separate juvenile specimens from adults when plotting abundance fluctuations may account for some of the observed discrepancies, as juveniles numbers explain much of overall fluctuations. A strong dependence of species life cycles on local parameters in mesic habitats may also explain the large differences observed, but this remains to be documented.

Damp riparian habitats are often distributed as small areas around springs, or narrow strips along streams, and their extent varies with water level. Strictly hydrophilous species are restricted to the permanently wet parts of these habitats which persist in the dry season, and to their immediate surroundings, sometimes reduced to a few centimetres fringe at the end of summer. The co-occurrence of hydrophilous and non-hydrophilous species may be linked to this spatial configuration on one hand, and to the permeability (sensu DEHARVENG & LEK 1995) of the hydrophilous assemblages on the other hand. The frequent disturbance of damp riparian habitats as a result of water level fluctuations is likely to prevent saturation of the springtail assemblages, allowing colonisation by species from neighbouring soil habitats. In flooding periods, hydrophilous species may actively migrate or be passively dispersed some distance from the permanently damp habitats, while non-hydrophilous ones may be washed into damp habitats as flood waters retreat, which may further explain the species mixing and the variable assemblage composition. Conversely, as water acts as a buffer for humidity and temperature, damp riparian habitats become suitable refugia during summer for many species of surrounding habitats (as observed by WEINER 1981 in Poland). This multi-causal influx of "outside" species brings the overall species richness of damp riparian habitat to high levels, comparable to those of the richest mesophilous habitats like forest litter (see DEHARVENG 1996 for Collembola of the same region).

Seasonal fluctuations of abundance were similar between the two studied springs for the hydrophilous component of the assemblages, but not for its non-hydrophilous component. Conversely, seasonal fluctuations of species

richness were very similar between the two studied springs for the non-hydrophilous component, but not for the hydrophilous component. Such a discrepancy may result from differences in species composition between hydrophilous and non-hydrophilous components of the assemblage. Abundance of the non-hydrophilous component results from the combined effect of a number of overlapping species cycles, which may locally blur climate-controlled fluctuations and explain the lack of congruence between site patterns. Conversely, the abundance of the hydrophilous component largely relies on the same single species (*Isotomurus cassagnau* alone accounted for 90.79 % of hydrophilous species abundance at La Maure, and 45.89 % at Ruau), which probably underlays overall between-site similarity. The different pattern of biodiversity fluctuations of the hydrophilous component between the two springs may simply reflect its lower dependence on broad scale ecological variables, as a consequence of life in a buffered environment, compared to non-hydrophilous species.

The non-hydrophilous Collembola which account for most of the site species richness are known to usually inhabit forest or meadow litter of the surrounding habitats. These mesophilous habitats are more diverse than damp habitats, because of larger temporal and spatial fluctuations of two key factors: temperature and humidity. Therefore, it could be expected that differences in the habitats surrounding the springs (stony versus non-stony substratum, meadow versus forest, hydric regime) would induce differences in temporal biodiversity patterns at the springs. On the contrary, the present study indicates that diversity fluctuations are correlated between the two sites, indirectly suggesting that regional climate tends to override site environmental differences. Correlation with local environmental factors supposed to be important for Collembola (CASSAGNAU 1961) remains particularly complex in our study. The main factor influencing springtail abundance that we identified (distance to water) had for instance an opposite effect at Ruau and La Maure. Another example is the fact that biodiversity was more related to distance to water at the decimetre scale than to water content of the substratum, although the latter is both more directly dependent on climatic conditions and considered to be more influential on collembolan life. Indeed, the modulation brought by local factors on the general driving climatic factors deserves deeper investigation.

Whatever the factors controlling seasonal patterns of abundance and biodiversity, the maintenance of a high level of non-hydrophilous species richness across seasons in damp habitats has important implications regarding ecosystem functioning. Damp riparian habitats act as refugia for non-hydrophilous Collembola and probably many other invertebrates during unfavourable periods. This feature, combined with the significant input of nutrients they contribute to aquatic communities (WARD et al. 1998), confers to them a central function in the dynamics of the larger terrestrial ecosystems in which they are nested. Damp riparian habitats are likely to represent much more in terms of



biodiversity and ecosystem functioning than their moderately diverse hydrophilous fauna and their limited extent alone would suggest.

### Acknowledgements

This work was supported by the European Union programme "High Endemism Areas, Endemic Biota and the Conservation of Biodiversity in Western Europe" (DG XII, Proposal n° PL931917). Anonymous reviewers and ERIC PATTEE provided very helpful comments and suggestions on an early draft of this paper.

### References

- BRETSCHKO, G. & CHRISTIAN, E. (1989): Collembola in the bed sediments of an Alpine gravel stream (Ritrodlat-Lunz Study Area, Austria). – *Int. Rev. ges. Hydrobiol.* **74**: 491–498.
- CARAPPELLI, A., FANCIULLI, P. P., FRATI, F. & DALLAI, R. (1995 a): The use of genetic markers for the diagnosis of sibling species in the genus *Isotomurus* (Insecta, Collembola). – *Boll. Zool.* **62**: 71–76.
- CARAPPELLI, A., FRATI, F., FANCIULLI, P. P. & DALLAI, R. (1995 b): Genetic differentiation of six sympatric species of *Isotomurus* (Collembola, Isotomidae); is there any difference in their microhabitat preference? – *Eur. J. Soil Biol.* **31**: 87–99.
- CASSAGNAU, P. (1961): *Ecologie du sol dans les Pyrénées centrales: les biocénoses de Collemboles.* – Hermann, Paris, 235 pp.
- (1987): A propos des types de coloration chez *Isotomurus palustris* (MÜLLER) (Collemboles). – *Rev. Ecol. Biol. Sol* **24**: 85–89.
- CASSAGNAU, P. & ROUQUET, O. (1962): Les Collemboles édaphiques du jardin botanique de Toulouse (France). Essai de Biocénologie Dynamique. – *Pedobiologia* **2**: 15–40.
- CHRISTIAN, E. (1986): Apterygota from terrestrial sand, gravel and debris accumulation in Austria. – Second Internat. Semin. Apterygota, Siena, pp. 139–141.
- CHRISTIANSEN, K. & BELLINGER, P. (1998): *The Collembola of North America, north of Rio Grande.* – Grinnell College Publ., Grinnell (Iowa), 1520 pp.
- COLWELL, R. K. & CODDINGTON, J. A. (1994): Estimating terrestrial biodiversity through extrapolation. – *Philos. Trans. Roy. Soc. London Ser. B – Biol.* **345**: 101–118.
- DEHARVENG, L. (1996): Soil Collembola diversity, endemism and reforestation: a case study in the Pyrenees (France). – *Conserv. Biol.* **10**: 74–84.
- DEHARVENG, L. & LEK, S. (1993): Remarques sur la morphologie et la taxonomie du genre *Isotomurus* BÖRNER, 1903 et description de deux espèces nouvelles de France (Collembola: Isotomidae). – *Ann. Soc. ent. Fr.* **29**: 245–259.
- (1995): High diversity and community permeability: the riparian Collembola (Insecta) of a Pyrenean massif. – *Hydrobiologia* **312**: 59–74.
- FRÄMBS, H. (1994): The importance of habitat structure and food supply for Carabid beetles (Coleoptera, Carabidae) in peat bogs. – *Memoirs Entom. Soc. Can.* **169**: 145–159.
- GIBERT, J. (1986): *Ecologie d'un système karstique Jurassien.* – Mémoires Biospéol. **13**: 1–377.
- GREGOIRE-WIBO, C. (1974): Bioécologie de *Folsomia quadrioculata* (Insecta, Collembola). – *Pedobiologia* **14**: 199–207.

- GREGORY, S. V., SWANSON, F. J., MCKEE, W. A. & CUMMINS, K. W. (1992): An ecosystem perspective of riparian zones. – *BioScience* **41**: 540–551.
- HALE, W. G. (1966): A population study of moorland Collembola. – *Pedobiologia* **6**: 65–99.
- HIJII, N. (1987): Seasonal changes in abundance and spatial distribution of the soil arthropods in a Japanese cedar (*Cryptomeria japonica* D. DON) plantation, with special reference to Collembola and Acarina. – *Ecol. Res.* **2**: 159–173.
- HOPKIN, S. P. (1997): *Biology of the Springtails (Insecta: Collembola)*. – Oxford University Press, 330 pp.
- JORDANA, R., ARBEA, J. & ARIÑO, A. H. (1990): Catálogo de colémbolos ibéricos. Base de datos. – *Public. Biol. Univers. Navarra. Serie Zoológica*, **21**: 1–231.
- KREBS, J. C. (1989): *Ecological methodology*. – Harper & Row, New York, 654 pp.
- MAGURRAN, A. (1988): *Ecological diversity and its measurement*. – Croom Helm, London, 179 pp.
- MASON, C. F. & MACDONALD, S. M. (1982): The input of terrestrial invertebrates from tree canopy to a stream. – *Freshwat. Biol.* **12**: 305–311.
- NOBLE-NESBITT, P. J. (1963): Transpiration in *Podura aquatica* L. (Collembola, Isotomidae) and the wetting properties of its cuticle. – *J. Exper. Biol.* **40**: 681–700.
- PEDIGO, L. P. (1970): Activity and local distribution of surface-active Collembola: II. Pond shore population. – *Ann. Ent. Soc. America*, **63**: 753–760.
- PICHARD, S., MASSOUD, Z. & ELKAÏM, B. (1989): Ecologie des peuplements de Collemboles de quelques mares et de leurs abords en région parisienne. – *Rev. Ecol. Biol. Sol* **26**: 451–472.
- PONGE, J. F. (1993): Biocenoses of Collembola in atlantic temperate grass-woodland ecosystems. – *Pedobiologia* **37**: 223–244.
- POZO, J., SELGA, D. & SIMON, J. C. (1986): Studies on the collembolan population of several plant communities of the Basque Country (Spain). – *Rev. Ecol. Biol. Sol* **23**: 215–232.
- PRAT, B. & MASSOUD, Z. (1981): Etude de la communauté des Collemboles dans un sol forestier. Evolution du peuplement. – *Rev. Ecol. Sol* **18**: 59–76.
- SKIDMORE, R. E. (1995): Checklist of Collembola (Insecta: Apterygota) of Canada and Alaska. – *Proc. Entomol. Soc. Ontario* **126**: 45–76.
- THIBAUD, J. M. (1970): Biologie et écologie des Collemboles Hypogastruridae édaphiques et cavernicoles. – *Mém. Mus. natl. Hist. nat.* **61**: 83–201.
- THOMAS, A. (1969): Sur l'importance des diptères dans l'environnement de quelques cours d'eau des Pyrénées. – *Ann. Limnologie* **5**: 61–71.
- VANDEL, A. (1960): Faune de France 64 – Isopodes Terrestres (première partie). – P. Lechevalier, Paris, 416 pp.
- VELLEMAN, P. F. (1997): *Data Desk Handbook version 6.0*. – Data Description inc. Publ., Ithaca (New York).
- WARD, J. V., BRETSCHKO, G., BRUNKE, M., DANIELOPOL, D., GIBERT, J., GONSER, T. & HILDREW, A. G. (1998): The boundaries of river systems: the metazoan perspective. – *Freshwat. Biol.* **40**: 531–569.
- WEINER, W. M. (1981): Collembola of the Pieniny National Park in Poland. – *Acta Zool. Cracov.* **25**: 417–500.

Submitted: 24 April 2001; accepted: 12 November 2001.

**Appendix.** Total number of springtails collected in La Maure and Ruau springs.

List in alphabetical order. H: hydrophilous species; unid.: unidentifiable (too young or damaged) specimens.

Species		La Maure	Ruau
<i>Arrhopalites</i> cf. <i>terricola</i> GISIN, 1958		8	0
<i>Arrhopalites</i> unid.		37	2
<i>Arrhopalites</i> sp.		3	1
<i>Bourletiella</i> sp.		4	1
<i>Brachystomella parvula</i> (SCHAEFFER 1896)	H	16	956
<i>Ceratophysella armata</i> (NICOLET 1841)		1	22
<i>Ceratophysella denticulata</i> (BAGNALL 1941)		0	1
<i>Ceratophysella engadinensis</i> (GISIN 1949)		3	1
<i>Ceratophysella</i> unid.		4	7
<i>Cryptopygus debilis</i> CASSAGNAU 1959		218	0
<i>Deutonura deficiens</i> DEHARVENG 1979		4	1
<i>Dicyrtomina minuta</i> (LINNAEUS 1967)		36	13
<i>Entomobrya</i> sp.		36	122
<i>Folsomia decopsis</i> STEINER 1958		245	15
<i>Folsomia manolachei</i> BAGNALL 1939		924	541
<i>Friezea cauchoisi</i> DELAMARE 1951		1	0
<i>Friezea claviseta</i> AXELSON 1900		0	1
<i>Friezea truncata</i> CASSAGNAU 1958		10	297
<i>Heteromurus major</i> MONIEZ 1889		0	2
<i>Hydroisotoma schaefferi</i> (KRAUSBAUER 1898)	H	0	2
<i>Isotomiella minor</i> (SCHAEFFER 1896)		1300	588
<i>Isotomurus balteatus</i> (REUTER 1876)	H	0	2
<i>Isotomurus cassagnai</i> DEHARVENG & LEK 1993	H	5679	2656
<i>Isotomurus catalanus</i> CASSAGNAU 1987	H	0	31
<i>Isotomurus nebulosus</i> LEK & CARAPELLI 1998	H	84	723
<i>Isotomurus prasinus</i> (REUTER 1891)	H	195	1227
<i>Isotomurus unifasciatus</i> (BOERNER 1901)	H	0	42
<i>Lepidocyrtus cyaneus</i> TULLBERG 1871		1	236
<i>Lepidocyrtus</i> unid.		26	255
<i>Lepidocyrtus lanuginosus</i> (GMELIN, 1788)		1	1
<i>Lepidocyrtus lignorum</i> (FABRICIUS 1793)		21	157
<i>Lepidocyrtus</i> sp.		0	1
<i>Megalothorax minimus</i> WILLEM 1900		109	9
<i>Megalothorax</i> sp. 2	H	263	94
<i>Mesaphorura</i> sp.		0	1
<i>Monobella grassei grassei</i> (DENIS 1923)		12	1
<i>Neanura muscorum</i> (TEMPLETON 1835)		0	1
<i>Oncopodura crassicornis</i> SHOEBOOTHAM 1911		47	0
<i>Onychiurus</i> gr. <i>minutus</i> DENIS 1932		0	12
<i>Onychiurus pseudogranulosus</i> GISIN 1951		423	483
<i>Parisotoma notabilis</i> (SCHAEFFER 1896)		224	151
<i>Protachorutes pyrenaicus</i> CASSAGNAU 1955		9	41
<i>Protaphorura armata</i> (TULLBERG 1869)		454	150
<i>Pseudachorutes palmiensis</i> BOERNER 1903		3	14

## Appendix. Continued.

Species		La Maure	Ruau
<i>Pseudachorutes parvulus</i> BOERNER 1901		3	9
<i>Pseudisotoma</i> sp. 1		10	564
<i>Pseudisotoma</i> sp. 2		8	372
<i>Pseudosinella alba</i> (PACKARD 1873)		63	51
<i>Pseudosinella duodecimoculata</i> BONET 1931		0	7
<i>Sminthuridae</i>		1	1
<i>Sminthurides</i> unid.		5	3
<i>Sminthurides malmgreni</i> (TULLBERG 1876)	H	6	21
<i>Sminthurides schoetti</i> AXELSON 1903	H	12	33
<i>Sminthurinus aureus</i> (LUBBOCK 1862)		18	5
<i>Sminthurinus signatus</i> (KRAUSBAUER 1898)		30	21
<i>Sminthurinus</i> sp.		18	0
<i>Sphaeridia pumilis</i> (KRAUSBAUER 1898)		161	4
<i>Stenaphorura</i> sp.		0	3
<i>Symphyleona</i> unid.		0	5
<i>Tomocerus minor</i> (LUBBOCK 1862)		235	105
<i>Tomocerus</i> sp.		0	2
<i>Vertagopus</i> sp.		0	5
<i>Willemia anophthalma</i> (BOERNER 1901)		0	2
<i>Xenylla</i> sp.		24	3
Total		10995	10076